

ANALYSIS OF STONE CRABS: *MENIPPE MERCENARIA*
(SAY), RESTRICTED, AND A PREVIOUSLY
UNRECOGNIZED SPECIES DESCRIBED
(DECAPODA: XANTHIDAE)

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Abstract.—The stone crab, *Menippe mercenaria* (Say, 1818) sensu lato, in the Caribbean and Carolinian Provinces of the western North Atlantic, is divisible into two morphologically distinct populations with almost separate, narrowly overlapping geographic ranges. These populations are here recognized as distinct species. The species differ in color, carapace morphometry, and stridulatory patches on chelae of the chelipeds. Five measured factors subjected to discriminant function analysis give good separation of the species at $P < 0.05$ for all specimens measured, and at $P < 0.01$ for specimens more than 15 mm in carapace length. *Menippe mercenaria*, restricted, ranges from Cape Lookout, North Carolina, through peninsular Florida, the Bahamas and Greater Antilles, to Yucatan peninsula, Mexico, and Belize. *Menippe adina*, new species, ranges from northwestern Florida around the Gulf of Mexico to Tamaulipas State, Mexico. The two species hybridize in the Apalachee Bay region of northwestern Florida.

Recent field studies in the Gulf of Mexico indicate that stone crabs assignable to *Menippe mercenaria* (Say, 1818), sensu lato, from the northwestern Gulf differ in color and morphometry from those found in peninsular Florida, and furthermore, that individuals exhibiting characters intermediate between these groups can be observed in the Apalachee Bay region of northwestern Florida. Questions arise from these recent surveys concerning variation over the range as a whole, i.e., whether the preliminary observations in the Gulf of Mexico were comprehensive enough to have validity, and whether still other populations within the range may exhibit character states with sufficient cohesion to be recognized as taxonomically distinct.

The chelipeds (claws) of this large crab are prized as a delicacy throughout a geo-

graphic range that extends through the Caribbean and Carolinian Provinces of the western North Atlantic Ocean from Cape Lookout, North Carolina, southward around peninsular Florida, through the Bahamas and Greater Antilles, to the Yucatan peninsula and Belize, and around the northern and western margin of the Gulf of Mexico to Tamaulipas State, Mexico, from intertidal burrows, crevices and pools, to a depth of 51 m (Williams 1984, in part). Through most of that range, the crabs are incidentally taken for human consumption as a byproduct of other fisheries, but along western and especially southwestern Florida, they are the basis for a seasonal commercial fishery (Costello et al. 1979). Since Florida record-keeping began in 1962-63, the fishery grew to a peak annual landing of 2.6 million lb of claws during the 1981-82 season, and thereafter declined somewhat (preliminary estimate by National Marine Fisheries Service, Southeast Fisheries Center, 1.7 million

¹ Order of authorship was decided by flip of a coin.

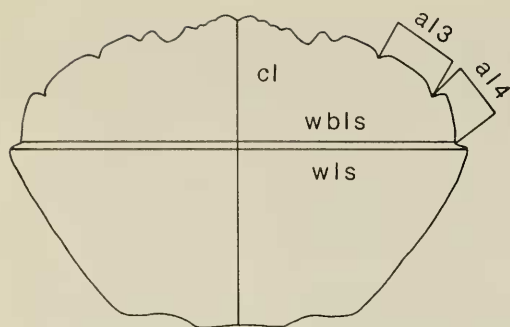


Fig. 1. Diagram of *Menippe mercenaria* (from Rathbun, 1884) showing carapace dimensions measured in mm: cl = carapace length in midline; wbls = width to base of lateral spine, wls = width between tips of lateral spines (wls - wbls = length of a/5); a/3 = width of anterolateral tooth 3, a/4 = width of anterolateral tooth 4.

lb for 1984-85). There is a sizeable fishery in Cuba as well where the crab is known as cangrejo moro (dappled crab).

Interrelationships of populations of these crabs seem important from standpoints of both biology and fisheries, and it is therefore the purpose of this paper to analyze the population structure from a systematic point of view. We have attempted to accomplish this by studying color and morphometry over selected parts of the range. Evaluation of these analyses demonstrates that two populations of the crabs can be distinguished. We interpret these populations to be two closely related species which hybridize in the panhandle region of northwestern Florida, and we give diagnostic characters for each in comparative tables, graphs, illustrations, and discussion.

Materials and Methods

General observations of color over the entire geographic range of the species were

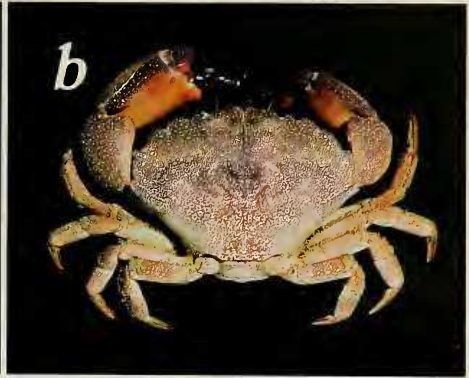


Fig. 2. Diagram showing inner surface of major chela bearing stridulatory patch, ♂ from USNM 7509, Key West, Florida.

accomplished by DLF, recorded photographically, and comparatively analyzed. Color pattern on the dactyl of the major chela was studied on specimens in the field, in museum collections, and on photographs by both of us. Measurements (Fig. 1) to the nearest 0.1 mm were recorded for carapace length in the midline, carapace width to the base of the notch between the 4th and 5th anterolateral teeth, carapace width including the 5th anterolateral tooth, and widths of the 3rd and 4th anterolateral teeth. Measurements of specimens from the northern Gulf of Mexico taken by DLF and of specimens in the crustacean collection of the National Museum of Natural History (USNM) taken by ABW were combined with a comparable data set from Charleston, South Carolina, plus a few measurements from specimens in other museums, photographs, and illustrations in literature, for combined statistical analysis. Density of parallel striae/mm in the stridulation patch on the inner surface of the major chela, and the maximum height of that chela, were recorded for representative populations by DLF (Fig. 2).

Statistical tests were performed on the Honeywell computer of the Smithsonian In-

Fig. 3. *Menippe adina*. Louisiana.— a, ♂ cw 61.7 mm, Bayou Fourchon, Fourchon Parish; b, ♀ unmeasured, Cameron, Cameron Parish. *M. adina* × *M. mercenaria*.— Florida: c, ♂ cw 92.2 mm, e, ♂ cw 64.6 mm, Wakulla Beach, Wakulla County; d, ♀ 102.7 mm, f, ♀ (ovig.) cw 86.8 mm, Turkey Point, Franklin County. *M. mercenaria*.— Florida: g, ♂ cw 99.4 mm, h, ♀ (ovig.) 92.6 mm, Turkey Point, Franklin County.



stitution, using the SPSSx data analysis system. A stepwise discriminant analysis of morphological variables was used in an attempt to separate hypothesized populations. The analysis included up to five morphological variables, each of which was a ratio (R1–R5) determined as follows (see Figs. 1 and 2):

R1—AL3/AL4

R2—AL4/CL

R3—WLS – WBLS/CL; WLS – WBLS
= length AL5 in Fig. 6C.

R4—WBLS/CL

R5—ln (no. striae per mm in stridulation patch/maximum height of chela); data for this ratio were log transformed because of strong curvilinear relationships.

Most specimens were assigned to either of two groups a priori on the basis of geographical distribution: Group 1, a warm temperate to tropical group ranging from North Carolina to Florida, Cuba, Yucatan-Belize, Saint Thomas, and perhaps Jamaica (*M. mercenaria*); Group 2, a northern Gulf of Mexico group ranging from extreme western Florida through the northwestern Gulf to northern Mexico (*M. adina*). The validity of these group assignments was investigated with discriminant analysis. The significance criterion used in this analysis was the overall multivariate F ratio for differences among group centroids. Morphological variables were selected stepwise for entry into the analysis on the basis of their partial F values. Unassigned specimens from two samples of questionable affinity (northwest Florida and Charleston, South Carolina) were independently entered into a classification analysis in order to determine their relationship to a priori groups on the basis of morphology. Most of the data set for the Charleston locality was limited to individuals larger than 15 mm carapace length and did not include counts of stridulatory ridges, so smaller individuals and R5 data were

excluded from comparative analysis of that sample.

Coloration was not included in the discriminant analysis, although it was scoreable for all fresh and most preserved specimens. Within the sample from northwest Florida, specimens were scored as color morph a—legs not banded, carapace without dark spots (typical of *M. adina*), b—legs banded, carapace without dark spots or with weak spots (intermediate), or c—legs distinctly banded, carapace with distinct dark spots (typical of *M. mercenaria*). Means and deviations of the morphometrically determined discriminant scores were calculated independently for each of these color morphs in order to compare trends in color with those in morphometry.

Specimens examined.—1 ♂, 1 ♀ from the Academy of Natural Sciences of Philadelphia (ANSP). 113 ♂, 127 ♀, 194 juv, from the National Museum of Natural History (USNM) are represented in the following list by catalog numbers without alphabetical prefix; those recorded by catalog number only are listed in Rathbun (1930:475–477). 114 ♂, 134 ♀ from cataloged lots in the University of Southwestern Louisiana Museum collection are listed with the alphabetical prefix USLZ. 2 ♂, 3 ♀ from the Florida Department of Natural Resources are listed with the alphabetical prefix FDNR.

Specimens or photographs of 20 ♂, 53 ♀ from other sources are appropriately indicated.

Synonymy.—The synonymies that follow are selective in that no attempt has been made to search for all references to *M. mercenaria* in textbooks, technical reports, popular works, and encyclopedias. Many such references are included in the primary sources cited.

Menippe mercenaria (Say), restricted
Figs. 1, 2, 3g–h, 4a–c

Cancer mercenaria Say, 1818:448.

Xanthe mercenaria.—H. Milne Edwards, 1834:399 (generic transfer).

- Pseudocarcinus ocellatus* H. Milne Edwards, 1834:409 (type locality unknown, type in Paris Museum).
- Xantho mercenaria*.—DeKay, 1844:4 (color, size, from South Carolina).
- Pseudocarcinus mercenarius*.—Gibbes, 1850:176 [12].
- Menippe mercenarius*.—R. Rathbun, 1884:772–774, pl. 264 (part, North Carolina-Florida); 1887:650–651 (part, North Carolina-Florida); 1893:772–774, pl. 264 (part, North Carolina-Florida).
- Menippe mercenaria*.—Stimpson, 1859:53–54 [7–8] (comparison with *M. nodifrons* and *M. obtusa*).—Coues, 1871:120 (North Carolina).—Kingsley, 1878:318 (part, North Carolina-Florida, not Panama).—A. Milne Edwards, 1879:262, pl. 47 (colored); pl. 48, fig. 32.—Enders, 1905:37 (in *Chaetopterus* tube).—Binford, 1913:147–202, pls. 1–9 (gametogenesis, mating).—Pearse, 1913:102–103 (North Carolina); 1929:231–233 (ecology).—Hay and Shore, 1918:439, pl. 35, fig. 8 (description, distribution).—Schroeder, 1924:49–50, fig. 23 (part, North Carolina-Yucatan).—Hyman, 1925:14, pl. 13, figs. 163–170 (larvae).—Rathbun, 1930:472, text-fig. 78, pls. 191–193 (description, distribution); 1935:117 (Pleistocene fossil).—Lunz, 1937:11, 21 (South Carolina).—Ayers, 1938:523–537 (oxygen consumption).—Chace, 1940:38 (Cuba).—Miner, 1950:522, pl. 167, unnumbered fig. (color description).—Siebenaler, 1952:99 (“trash” in trawls).—Stephenson and Stephenson, 1952:36 (in Carolinian region).—Menzel, 1956:80 (part, Apalachee Bay, Fla.).—Springer and Bullis, 1956:19 (part, sta 933 off W Florida).—Vernberg, 1956:227–ff. (oxygen consumption of tissues).—Gray, 1957:35–ff. (gill area).—Costlow and Bookhout, 1960:212 (method for hatching eggs).—Guinot-Dumortier and Dumortier, 1960:129–130, fig. 10 (stridulation structures).—Porter, 1960:168–ff., figs. 1–3 (larval development).—Manning, 1961:273–ff. (growth stages).—Tabb and Manning, 1961:600 (S Florida); 1962:44–46, 48, 61 (S Florida).—Rees, 1963:6, fig. 8 (general notes).—Dragovich and Kelly, 1964:83 (Tampa Bay).—Bullis and Thompson, 1965:12 (part, off SE Florida, Tampa Bay, and Golfo de Campeche).—Clark, 1965:52–54 (on turtle).—Gunter and Hall, 1965:64, 67 (SW Florida).—Williams, 1965:183, figs. 164D, E; 166 (part, not NW Gulf of Mexico).—Futch, 1966:1–6, figs. 1–3, 6 (part, not NW Florida).—Karandieva and Silva Lee, 1966:5–19 (respiration & osmoregulation, Cuba); also translation 1973:292–310.—Sushchenya and Claro, 1966:217–230 (metabolism); also translation 1973:311–335.—Sushchenya and Claro Madruga, 1967:75–97 (energetics).—Bliss, 1968:369 (water loss in air).—Cheung, 1968:117–120, 1 pl. (sperm retention).—Savage and McMahan, 1968:1–17, figs. 9–11 (juvenile growth).—Cheung, 1969:327–346 (growth & reproduction in Florida).—Hartnoll, 1969:162–ff. (mating).—Herreid, 1969:831, ff. (water loss); 1969a:424–428 (integument permeability).—Suárez Alvarez and Xiqués Diaz, 1969:155 (physiology of feeding).—Ong and Costlow, 1970:17–29 (larval development).—Hudson et al., 1970:9 (list, Florida Bay).—Kurata, 1970:209–212, pls. 73–74 (development).—Rouse, 1970:144 (S Florida).—Bender, 1971:11 (abstract, oxygen consumption, juveniles).—Dudley and Judy, 1971:3–ff. (planktonic larvae).—Lyons et al., 1971:34 (Florida).—Savage, 1971:315–316, pl. 1 (mating); 1971a:1–19, fig. 3 (rearing experiments).—Suárez Alvarez and Xiqués Diaz, 1971:279–281 (physiology).—Bardach et al., 1972:672 (short review, culture).—Yang, 1971:53–54 (larval culture methods).—Bookhout and Costlow, 1972:1–13 (pollutant effect, larval development).—Bookhout et al., 1972:166–ff. (pesticide & larvae).—Stewart, 1972:173–178 (thermal effluent, mariculture).—Yang, 1972:183–184 (reproduction in Florida, general).—Cheung,

- 1973:1-11 (regeneration).—Collard and D'Asaro, 1973:fig. III G3 (part), fig. III G4, G7 (part) (habitats in eastern Gulf of Mexico).—Eguchi and Waterman, 1973:146, 154 (reticular cell, comparison).—Leffler, 1973:1047, ff. (metabolic rate & body size).—Sushchenya and Claro, 1973:311-335 (energy & growth).—Bland and Amerson, 1974:232-235 (experimental egg infection).—Bookhout and Costlow, 1974:77-87 (sublethal effects, mirex, larvae).—Duke and Dumas, 1974:152 (pesticide effect, larvae, review).—Grizzle, 1974:136 (Florida).—Mootz and Epifanio, 1974:44-55 (larval energy budget).—Payen, 1974:214-225, figs. 2, 4c (sexual morphogenesis in megalopa).—Sandifer et al., 1974:55-59 (aquaculture contaminants).—Savage et al., 1974:1-5, figs. 1-5 (molting).—Zeiller, 1974:94 (color photo).—Perry, 1975:55 (occurrence in *Callinectes* fishery).—Savage et al., 1975:1-37 (Florida fishery).—Cheung, 1976:138-144 (claw regeneration, functional change).—Gore et al., 1976:286 (Florida).—Iversen and Beardsley, 1976:195-196 (shell disease).—Miller, 1976:630 (Florida fishery).—Yang and Krantz, 1976:1-15 (culture manual).—Costlow, 1977:452-453 (pesticide & larvae).—Forward, 1977:331-341 (shadow response, larvae).—Kinne, 1977:839-840, 874, 876 (larval culture).—Livingston et al., 1977:90, Table 3 (part, Apalachicola Bay, Fla.).—Sinclair, 1977:193-207 (agonistic behavior).—Warner, 1977:174 (claws & trap fishery). Bert et al., 1978:1-82 (biology).—Gore et al., 1978:225-ff. (reefs, SE Florida).—Savage and Sullivan, 1978:1-23 (growth & claw regeneration).—Tucker, 1978:169-172 (amino-acids, larvae).—Whetstone and Eversole, 1978:42-48 (predation on hard clams).—Young, 1978:182 (South Carolina).—Brown et al., 1979:143-159 (biomechanics, chelipeds).—Costello et al., 1979:19450-19496 (comprehensive review, part, from Cedar Key, Fla. S), fig. 1.—Costlow, 1979:356-357, 360-361 (pesticide & larvae).—Pérez Pérez and Ros, 1979:1-33 (regional Cuban fishery).—Roberts et al., 1979:419-430 (dinoflagellate toxic effects).—Schlieder, 1980:695-700 (desiccation, autospasy & egg production).—Sullivan, 1979:1-37 (population in SW Florida).—Williams and Duke, 1979:173, 183-185 (part, life history & ecology), 194, 200, 203, 205 (review pesticide effects).—Barnes, 1980:728, fig. 14-55I (photo).—Davis et al., 1980:1-23 (mortality, declawing).—Factor, 1980:843 (larval development, mandibles & gastric mill).—Goy and Costlow, 1980:888 (larval nutrition).—McConaughy et al., 1980:544-547 (winter induced mating).—Ros and Suárez, 1980:5-17 (epibiosis).—Ros et al., 1980:175-196 (polychromatism).—Ros Pichss et al., 1980:71 (reproduction, abstract).—Ros Pichss et al., 1980:72 (ovulation cycles, abstract).—Simonson and Steele, 1980:6 (abstract).—Sulkin and Van Heukelem, 1980:91-96 (larval diet).—Zuboy and Snell, 1980:1-32 (Florida fishery assessment).—Anger et al., 1981:199-212 (starvation, zoeae).—Anger et al., 1981a:518-525 (starvation resistance, zoeae).—Brine and Austin, 1981:283-286 (chitin variability).—Brine and Austin, 1981a:173-178 (chitin isolates).—Factor, 1981:253-258 (basement membrane, mid-gut); 1981a:1002 (basement membrane, mid-gut).—Meinroth, 1981:647 (part, not color pl. 642, N. America).—Pérez and Briquets, 1981:30-43 (size-class sampling methods).—Ros and Quiñones, 1981:92-102 (teratology).—Ros et al., 1981:1-29 (ovulation cycles).—Ros et al., 1981:73-91 (fecundity).—Simonson and Steele, 1981:21-28, figs. 1-5 (claw asymmetry, reversal & regeneration).—Factor, 1982:299-312 (development & metamorphosis feeding apparatus).—Lee et al., 1982:145-159 (oxygenase system).—Ortiz and

- Pol Paredes, 1982:39–59 (symbionts & food).—Ramos Trujillo, 1982:97–115 (organic reserve in muscle).—Ros and Quiñones, 1982:17–24 (lipids in tissues).—Telford, 1982:166, fig. 5 (list, coral reef fauna).—Zuboy and Snell, 1982:1–21 (Florida fishery assessment).—Wenner and Stokes, 1983:1–28 (experimental fishery, chela size & regeneration).—Lindberg and Marshall, 1984:1–18 (part, peninsular Florida population).—Roer and Dillaman, 1984:900, ff., pl. 2, figs. 9–12, pl. 3, figs. 15–20 (SEM views, cuticle).—Williams, 1984:420 (part, not NW Gulf of Mexico).—Felder et al., 1985:199 (color during development).—Simonson, 1985:281–293, figs. 1–2 (regeneration).—Bert et al., 1986:1–77 (South Florida population dynamics).—Salmon et al., 1986:29, Table 2 (hatching rhythms).
- Menippe rumphii*.—Stimpson, 1871:106 [6] (Florida, striations on inner palm). [Not *M. rumphii*.]
- Menippe ocellata*.—von Martens, 1872:87.
- Menipe ocellata*.—Gundlach and Torralbas, 1900:368 (not fig. G).—Gundlach et al., 1917:563 [23] (not fig. 15) (Cuba).
- Material*.—North Carolina: 17527, 62527.
- South Carolina: 2089, 17170, 32250, 17171, 4906, 26144, 18195.—228714. 2 ♂, 1 ♀; Folly River, Charleston, M. Caldwell, 5–6 Apr 1986, 18.8–18.9° C, 30‰.—Uncataloged measured specimens from Charleston, 19 ♂, 51 ♀.
- Georgia: 19474.—170782. 1 ♀; Sapelo Sound, M. Gray, 13 Dec 1962.—170784. 2 ♂, 1 ♀; same, 26 Jan 1962.—170783. 1 ♂, 3 ♀; Raccoon Bluff, M. Gray, 18 Feb 1961.
- Florida: 56829, 20097, 2094, 20095, 42129, 53754, 6370, 8964, 18520, 7509 (6 ♂, 4 ♀ in 1985), 20096, 33463, 57007, 15101, 53756, 6948, 14988, 6439, 50465, 56359, 25607, 25608, 14995, 2017, 14991, 6432, 56830, 14989, 14997, 53757, 26145, 26146, 14992, 57843, 14994, 6409, 60973, 53755.—75792. 1 juv; Fernandina, rocks on jetty at Cumberland Sound, A. Pizzini, 13 Jul 1934.—170004. 1 ♂, 1 juv; Indian River County, Sebastian Inlet on intertidal sabellariid reef S side inlet bridge, R. H. Gore, 1 Nov 1974.—170005. 1 ♂; same, 15 Jul 1974.—170006. 1 ♂, 1 ♀, 1 juv; same, 9 Dec 1974.—170007. 1 ♀ (ovig.), 1 juv; St. Lucie County, Ft. Pierce Inlet intertidal sabellariid reef, R. H. Gore, 19 Aug 1974.—228511. 1 ♂; Biscayne Bay, Key Biscayne, SW Point flats, 25°41'18"N, 80°10'48"W, 2 ft, C. A. Child, summer 1962.—75785. 1 ♂ juv; Key West, W. C. Schroeder, 12 Nov 1919.—75786. 1 ♂, 2 juv; Key West, W. K. Butts, 28 Aug–4 Sep 1919.—75788. 1 ♂ juv; Key West in sponge, D.R.C. from USBF.—75796. 1 ♂, 1 ♀; Key West from USBF.—15570. 1 ♂; Lee County, Sanibel Island, N end beach, R. B. Manning, 3 Apr 1972.—97501. 1 ♂, Gulf of Mexico, 27°36'N, 83°18'W, 20 fm, Oregon sta 933, S. Springer, 18 Mar 1954.—101478. 1 ♂ juv; Gulf of Mexico, 27°30'N, 82°46'W, 3 fm, Silver Bay sta 59, 17 Jul 1957.—101479. 1 juv; Gulf of Mexico, 27°11'N, 82°33'W, 3 fm, Silver Bay sta 60, 17 Jul 1957.—72854. 9 juv (one soft shell); Lemon Bay, Englewood, S. Springer, Bass Biol. Lab., 2 Feb 1936.—75791. 1 juv; shore Sarasota Bay, W. W. Wallis, summer 1930.—FDNR, I-7654. 1 ♂, 2 ♀; Citrus County off Crystal River.—FDNR, I-7695. 1 ♂, 1 ♀; same.—99861. 1 ♂, Cedar Key, main channel, D. K. Caldwell, 23 Feb 1955.
- Bahamas: 88662. 2 ♂, Bimini, A. S. Pearse, 10 Nov 1948.
- Cuba: 61114.—47901. 1 ♀; Los Arroyos, Thos. Barreras, May 1914.—216981, 1 ♀; near Varadero Beach, SE Hicacos Peninsula at 2 km marker, R. B. Manning et al., 2 Mar 1978.—216982. 3 ♀; E of Batabano, S shore, 4–5 m, R. B. Manning et al., 3 Mar 1978.—Museum of Comparative Zoology, Harvard University 10916. 1 ♀; Cienfuegos, off dock in fish trap, 30 Mar 1939.—Photographs of *M. ocellata* ♂ collected by M. Gundlach,

Muséum National d'Histoire Naturelle, Paris.

St. Thomas, Virgin Islands: Photographs of *M. ocellata* ♀ collected by M. Souffait, Paris Museum.

Jamaica: 62528.

Mexico: 57067.—USLZ2945. 2 ♂, 1 ♀; near Progreso, State of Yucatan, D. L. Felder, 9 Jan 1978.—USLZ2946. 2 ♂, 2 ♀; same.—90343. 1 ♀, 1 juv; Campeche, State of Campeche, C. J. Goodnight, 20 Jul 1949.—USLZ2937. 1 ♂, 1 ♀; NE of Champoton, State of Campeche, T. C. Shirley and R. Tinnin, 3 Jan 1973.—USLZ2944. 1 ♂; just north of Seybaplaya, State of Campeche, D. L. Felder, 6 Jan 1978.—USLZ2940. 2 ♀; NE of Champoton, State of Campeche, D. L. Felder, 7 Jan 1978.—USLZ2943. 2 ♂, 3 ♀; same, 6 Jan 1978.—USLZ1413. 1 ♂; Isla Aguada, State of Campeche, D. L. Felder, 5 Mar 1981.—USLZ2939. 1 ♂; same, 5 Jan 1978.—USLZ2941. 2 ♂, 4 ♀; same.—USLZ2942. 2 ♂, 2 ♀; same.—USLZ2947. 1 ♂; same.—USLZ2948. 2 ♂, 1 ♀; same, 1 Jun 1982.

Belize: 204232. 2 ♂; Cay Caulker, Blue Hole, W side Cay Virgil, H. O. Wright, 8 Feb 1973.

Diagnosis.—See Table 1.

Type locality.—“*Inhabits* the southern states.” Say’s original account of *M. mercenaria* gave only a general indication of geographic origin for his material, but the last paragraph stated, “Esteemed as food and sold in the Charleston market, tied up in small parcels from four to eight together.” Weiss and Ziegler (1931) recounted the collecting trip organized by Say and others in autumn 1817 for visits to the sea islands and adjoining coast of Georgia, and passage for an indeterminate distance up the St. John’s River, Florida, that was cut short by bad feeling between the United States and Indian tribes in Florida, then still under control of Spain. The party retraced their route, touching Savannah and Charleston. The dates of this expedition and Say’s de-

scriptive account leave almost no doubt that his material came from the southeastern Atlantic coast of the United States.

Types.—Say listed his specimens as “Cabinet of the Academy.” There are only two specimens of *Menippe mercenaria* in the ANSP. These are now numbered 3246 (dry). 1 ♀; cl 78 mm, cw 114.7 mm, maximum height of major right chela 50.1 mm, striae in patch 3/mm, maximum height of minor left chela 49.3 mm; 1 ♂, cl 64.8 mm, cw 96.2 (estimated, right lateral spine broken), maximum height of major right chela 45.1 mm, striae in patch 3/mm but very worn, maximum height left minor chela 19.6 mm (regenerated). The specimens each bear the number 26, printed by press in black ink on a tiny square of white paper that is affixed near the center of the carapace with sealing wax. This was the method of numbering individual specimens in early days of the Academy, and this was one of the very early numbers assigned.

The evidence indicates that these specimens are syntypes of Say’s *Cancer mercenaria*, in both our opinion and that of curators at the ANSP. Say’s original description was general with respect to morphology, but he did give details on color of the fingers, structure of the male abdomen, measurements of one specimen, and other comments. The female bears the handwritten words *Cancer mercenaria* in very old brownish colored ink on the upper outer propodal surface of the right cheliped. Measurements of this specimen are almost exactly those given in the original description, “Length three inches and one fourth, breadth four inches and a half,” (the length measured by calipers is now 1/8 inch less). Say did not mention the sex of the measured individual. Other labels with these specimens, “*Pseudocarcinus mercenarius*, ♂ ♀ Southern coast of N.A.,” “26a & b” (in brownish ink) along with the pencilled name “*Pseudocarcinus mercenaria*,” as well as other pencilled emendations, are attrib-

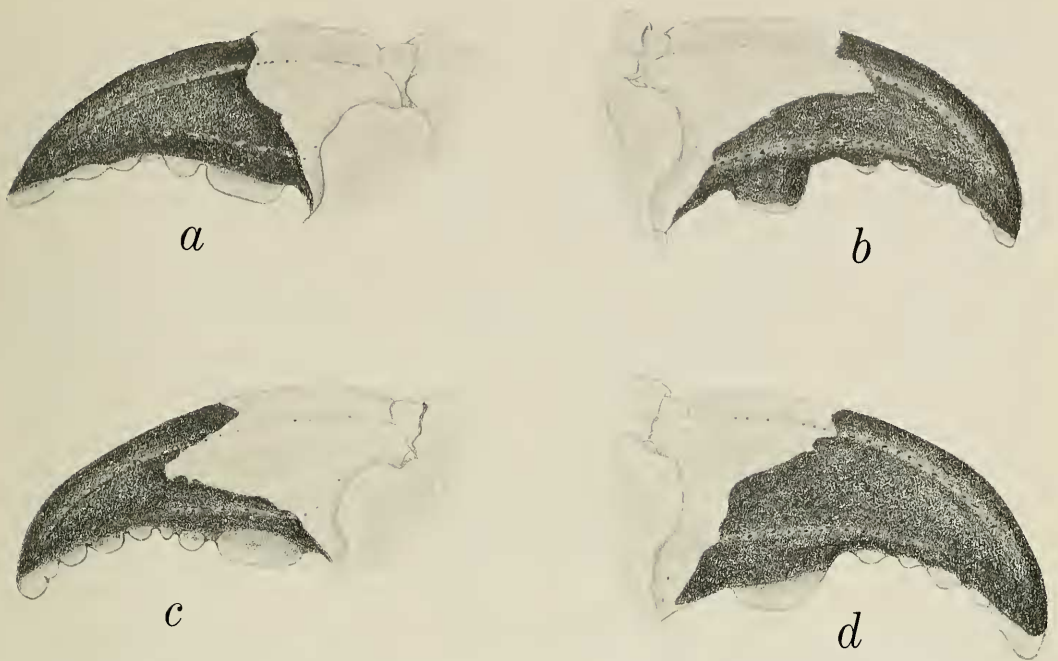


Fig. 4. Representative color patterns on frontal surface of dactyls of major chelae (see Table 1). *M. mercenaria*, light color preceding border between light and dark areas variously extended below punctate groove as broad tongue: a, 17171, Charleston, S.C.; b, 7509, Key West, Fla.; c, 47901, Cuba. *M. adina*, same extended along punctate groove as narrow point: d, 72139, Texas.

able to subsequent workers. No attempt has been made to determine who made such additions or changes.

Both specimens are in good condition for dry preservation of nearly 170 years. The chelipeds of both are still attached, although some of the succeeding pereopods are disarticulated, broken or missing. The exoskeleton of the female is clean. That of the male bears scattered barnacles on the carapace and on the carpus and propodus of the major cheliped which seems disproportionately large for a specimen with that size cephalothorax. Both the encrustation of the male and obvious wear on teeth of its major chela and stridulation patch indicate advanced duration of the instar. The major dactyl of each specimen has a color pattern about halfway intermediate between that shown in Fig. 4a and c for *M. mercenaria*.

This alone testifies to origin in the Carolinian region.

Known range.—Cape Lookout, North Carolina, southward around peninsular Florida to Wakulla County, northwestern Florida, through the Bahamas and Greater Antilles to St. Thomas, Virgin Islands, Yucatan peninsula to southwestern State of Campeche, Mexico, and to Belize (Fig. 5). Intertidal to 51 m.

Menippe adina, new species
Figs. 3a–b, 4d

Menippe mercenarius.—R. Rathbun, 1884: 772–774, pl. 264 (part, northern Gulf of Mexico); 1887:650–651 (part, northern Gulf of Mexico); 1893:772–774, pl. 264 (part, northern Gulf of Mexico).

Menippe mercenaria.—Cary and Spauld-

Table 1.—Comparisons between two species of *Menippe*.

Structure	<i>M. mercenaria</i>	<i>M. adina</i>
COLOR		
Carapace	Poorly defined light yellow spots on broken pattern of reddish-orange to reddish-violet, and often with additional dark spots; latter ocellated and near black in young.	Light yellow spots or flecks on broken pattern of reddish-orange to reddish-violet; spots edged with darker pigment in young.
Chelipeds	Frontal surface of major dactyl having border between light area at base and dark distal part <i>usually</i> with light area extended below punctate groove as broad tongue; often nearly vertical (see Table 2).	Frontal surface of major dactyl having border between light area at base and dark distal part <i>usually</i> with light area extended along punctate groove as narrow point; rarely almost vertical (see Table 2).
Legs	Carpi and propodi distinctly banded with reddish-brown to orange (some bands maroon); ground color lighter (more broken mottling) between dark bands; without broken line of light spots at midwidth of merus 5.	Carpi and propodi lacking distinct bands; ground color reddish-orange to wine; pale yellow spots in longitudinal broken line at midwidth of merus 5.
MORPHOLOGY		
Anterolateral tooth 3	Almost always broader than 4, rarely equal to.	Usually broader than 4, but often narrower than and sometimes equal to.
Anterolateral tooth 5	Weakly prominent, somewhat blunt; anterior margin shallowly concave, tip directed more laterally than anteriorly.	Strong, prominent, fairly acute; anterior margin rather strongly concave, tip directed more anteriorly than laterally.
Posterolateral margin of carapace	Usually weakly convex in anterior 1/3.	Usually straight to concave in anterior 1/3.
Setae on legs 2-5	Dorsal margin of meri usually with few if any; sparse on propodus 5, restricted distally.	Dorsal margin of meri usually with well defined row; dense along most of ventral margin on propodus 5.

ing, 1909:12 (Louisiana).—Schroeder, 1924:49–50, fig. 23 (part, Texas).—Reed, 1941:44 (as *Manippe*), 73 (Texas).—Behre, 1950:24 (Louisiana).—Gunter, 1950:38 (temperature, salinity, habitat, Tex.).—Whitten et al., 1950:59, 64, 71 (Texas jetties).—Hedgpeth, 1953:172, 175 (oyster biocoenosis, etc.).—Walker, 1953:204 (Louisiana).—Hildebrand, 1954:276 (Texas).—Wass, 1955:157 (Alligator Harbor, Fla., color).—Menzel, 1956:80 (part, Apalachee Bay, Fla.).—Menzel and Hopkins, 1956:177–184, fig. 1 (predator on oysters).—Parker, 1956:319 (Miss. Delta).—Springer and Bullis, 1956:19

(part, Apalachee Bay, Fla.).—Simmons, 1957:179, 191 (in 25–35‰ S, upper Laguna Madre, Tex.).—Menzel and Nichy, 1958:125, 140–141, 144, fig. 6 (predator on oysters).—Parker, 1959:2123, 2161 (Texas).—Pounds, 1961:23, 46, figs. unnumbered on p. 23, 14, pl. 9, fig. 3 (natural history).—Richmond, 1962:75 (occ. Horn Is., Miss.).—Leary, 1964 (reissued 1967):23, 46, figs. unnumbered on p. 23, 39, fig. 14 (natural history).—Bullis and Thompson, 1965:12 (part, in and near Apalachicola Bay, Fla.).—Williams, 1965:183 (part, not Carolina-Florida-Yucatan population).—Futch, 1966:1–6 (part, not

peninsular Florida).—Menzel et al., 1966: 86, 90 (oyster predator).—Powell and Gunter, 1968:285–299 (natural history).—Lindner and Cook, 1971:157–162 (larval rearing, Texas).—Perret et al., 1971:62, appendix Tables 4, 7 (temperature, salinity, size trawl catch, La.).—Hoese, 1972:40 (Chandeleur Is., La.).—Collard and D'Asaro, 1973:fig. III G3 (part), fig. III G7 (part) (habitats, eastern Gulf of Mexico).—Christmas and Langley, 1973:295 (temperature, salinity, habitat, Miss.).—Day et al., 1971:23, 39 (Louisiana).—Felder, 1973:64–65, pl. 9, figs. 2–3 (NW Gulf of Mexico, key).—Fotheringham and Brunenmeister, 1975: 17, 26, 114, 136, 149, 167, figs. 2.3, 6.9 (mislabelled as *Panopeus herbstii*) (habitat, feeding).—Juneau, 1975:42 (low salinity, La.).—Perry, 1975:55 (occ. *Callinectes* fishery, Miss.).—Miller, 1976:630 (conservation, fishery).—Livingston et al., 1977:90, Table 3 (part, Apalachicola Bay, Fla.).—Burden, 1978:129 (temperature, salinity, habitat, La.).—Costello et al., 1979:19450–19496 (part, comprehensive rev., Apalachicola Bay, Fla. westward to Mexico).—Williams and Duke, 1979: 183–185 (part, life history, ecology).—Meinroth, 1981:647 (part, color pl. 642, N. America).—Mauro and Mangum, 1982:189–195 (temperature and respiratory physiology, specimens may be hybrids).—Kent, 1983:257–283 (predation on whelks, crabs may be hybrids).—Lindberg and Marshall, 1984:1 (northern Gulf of Mexico population).—Williams, 1984: 420 (part, not Carolina-Florida-Yucatan population).—Brooks and Mariscal, 1985: 112–116 (feeding on hermit crabs).—Horst and Bankston, 1986:1–20 (Louisiana fishery potential).

Menippe nodifrons Stimpson.—Rathbun, 1930:479 (part, USNM 30566 from Louisiana).—Scotto, 1979:359 (Louisiana).

Material.—Florida: USLZ1651. 1 ♂; Panama City, D. L. Felder.—USLZ258. 1 ♀;

Table 2.—Color pattern on frontal surface of dactyl of major chela in three populations expressed as percent of total sample. Patterns based upon shape of border between light proximal and dark distal coloration and classified by location of apical part of light coloration which may be: a corner or point marking punctate groove (on groove); a broad extension below punctate groove (below groove); or an irregular pattern without an apical extension (irregular/absent), in which border between colors may be nearly vertical (see Fig. 4).

Population	On groove	Irregular/absent	Below groove
Carolina-Belize n = 123	27.6	21.1	51.2
Cedar Keys to Apalachicola Bay, Fla. n = 88	46.6	19.3	34.1
NW Gulf of Mexico n = 156	94.9	5.1	0

same.—USLZ2860. 1 ♂; same.—USLZ2676. 2 ♂; St. Andrew Bay, Panama City.—FDNR, I-2947. 5 ♂, 1 ♀; Saint Andrew Bay, Magnolia Beach to jetty and wreck N of jetty, Panama City, Bay County, 3 Jul 1966.—99871. 1 ♀ juv; Pensacola, Intracoastal Waterway 3.5 mi E Interarity Point, F. Berry and A. Mead, 15 Aug 1953.

Alabama: 19355.—81444. 1 ♂ juv; Mobile Bay, 30 Jan 1938. USLZ885. 1 ♀; Dauphin Island, J. W. Martin, 11 Nov 1977.

Louisiana: 26147.—64142. 1 ♂; Grand Pass, Lake Borgne, S. Springer.—USLZ83. 1 ♀; S Breton Island, Nov 1969.—USLZ2949. 1 ♂, 1 ♀, juvs; California Bay, D. L. Felder, 28 Mar 1972.—USLZ2685. 1 ♂; Lake Grande Ecaille, W. W. Forman and L. J. Kennair, 5 May 1972.—USLZ2686. 2 ♂, 2 ♀, juv; Lake Grande Ecaille, D. L. Felder, 8 May 1973.—USLZ2690. 1 ♂, 2 ♀; Grand Terre Island, C. Dugas, 12 Oct 1982.—USLZ 2691. 2 ♂, 7 ♀; same, 9 Nov 1982.—USLZ2692. 3 ♂, 2 ♀; same.—USLZ2693. 3 ♂, 7 ♀; same, 16 Nov 1982.—USLZ2694. 5 ♂, 4 ♀; same, 2 Dec 1982.—USLZ2696. 1 ♂, 7 ♀; same, 30 Nov 1982.—USLZ2697. 6 ♂, 6 ♀; same, 18 Nov 1982.—USLZ2698. 2 ♂, 6 ♀; same.—USLZ2699. 5 ♂, 11 ♀; same.—

USLZ2700. PARATYPES: 1 ♂; transferred to USNM 228864. 1 ♂, 5 ♀; same, 28 Oct 1982.—USLZ2701. PARATYPES: 1 ♂, 1 ♀; transferred to USNM 228861. HOLOTYPE ♂, (cl 75.4 mm, width between lateral spines 113.6, width to base lateral spines 106.5); USNM 228862. ALLOTYPE ♀ (cl 70.8 mm, width between lateral spines 102.8, width to base of lateral spines 98.7); PARATYPES: USNM 228863. 5 ♂, 7 ♀; same, 8 Oct 1982.—USLZ2695. 1 ♀; Grand Terre Island, J. M. Howell and F. M. Truesdale, Aug 1983.—USLZ1086. 1 ♀; Barataria Bay, L. P. Rozas, 21 Oct 1979.—USLZ1783. 1 ♂, 1 ♀; Barataria Bay.—102896. 2 juv; Barataria Bay, Grand Isle, E. H. Behre, 19 Aug 1943.—103756. 1 juv; from fouling collectors, 7.5 fm, S Grand Isle, E. H. Behre, 7 Jul 1959.—103757. 2 juv; same, C. E. Dawson, 3 Aug 1959.—103758, 3 juv; same, C. E. Dawson, 14 Sep 1959.—USLZ72. 1 ♀; Grand Isle, 1969.—USLZ2688. 1 ♂; near mouth of Bayou Fourchon, R. W. Heard III, Jun 1982.—USLZ2687. 1 ♂, 1 ♀; Freeport Sulphur Production Platform off Grand Isle, D. L. Felder, Nov 1971.—189917. 1 ♂; Bay Marchand Lease Area, 29°02'50"N, 90°09'46"W, 20 ft, SwRI for BLM, 19 Jun 1978.—187001. 1 ♀; South Timbalier Lease Area, 500 m N of platform, 28°48'19"N, 90°36'29"W, 18 m, SwRI for BLM, otter trawl, 25 Aug 1978.—30566. 1 ♂; Cameron (as *M. nodifrons* in Rathbun [1930]); R. P. Cowles.—USLZ2689. 1 ♀; Cameron rock jetties, J. Kavanagh, M. LaSalle, and T. Bishop, 30 Sep 1979.—USLZ1085. 1 ♀; same.—USLZ1818. 1 ♀; same.—USLZ358. 1 ♂; off Holly Beach, E. B. Stueben, trawl, 4 Aug 1973.—USLZ750. 2 ♀; between Holly Beach and Peveto Beach, C. Boudreaux, 9 Nov 1968.

Texas: 20637, 33032.—71664. 1 ♂; Texas, C. T. Reed.—72130. 1 ♀; Gulf Coast, South-Western Biol. Supply Co.—72139. 1 ♂; same.—78395. 1 ♂, 1 ♀; Galveston Bay, C. E. Burt, 9 Apr 1939.—USLZ96. 1 ♀; Freeport, J. Fruge, 1 Nov 1969.—USLZ686. 1 ♀; Port Aransas, J. Holmquist, 20 Jul 1977.—

USLZ2681. 2 ♀; Port Aransas, T. C. Shirley and S. C. Rabalais, 14 Aug 1972.—62735. 1 ♀; Corpus Christi, M. E. Quisenberry, 1929.—72188. 1 ♀; Corpus Christi Bay, H. B. Parks, Oct 1936.—USLZ2935. 1 ♂; Corpus Christi Bay, T. C. Shirley, 18 Feb 1972.—USLZ2684. 1 ♀; jetty at Corpus Christi fish pass, D. L. Felder, 14 Aug 1972. USLZ685. 1 ♂, 3 ♀; S Padre Island rock jetty, Cameron County, J. Holmquist 22 Jul 1977.—USLZ2682. 1 ♀, many juv; same, S. C. Rabalais and N. N. Rabalais, 29 Jun 1973.—USLZ2683. 1 ♂; same, D. L. Felder, 28 May 1979.—USLZ2934. 1 ♂; Mansfield Pass rock jetty, S. C. Rabalais and N. N. Rabalais, 14 Jul 1973.—USLZ2932. 1 ♂, 1 ♀; S Padre Island rock jetty, Cameron Co., D. L. Felder, 28 May 1979.

Mexico: USLZ2938. 1 ♂; Barra del Tordo, mouth of Rio Carrizal, ca 75 km N Tampico, State of Tamaulipas, D. L. Felder, 24 May 1982.

Diagnosis.—See Table 1.

Type locality.—Grand Terre Island, Louisiana. See *Material*.

Known range.—Wakulla County in northwestern Florida, westward and southward around Gulf of Mexico to Tamaulipas State, Mexico (Fig. 5). Intertidal to 14.6 m (Hildebrand 1954).

Etymology.—From the Greek *adinus* (adinos), close, crowded, with reference to the patch of closely crowded striae on the inner palmar surface of the major chela.

Introggressive Zone: *Menippe adina*,
M. mercenaria, and
M. adina × *M. mercenaria*
Fig. 3c–f

Material.—Florida: 56383.—92357. 1 ♀; Gulf of Mexico, 29°03'N, 84°24'W, 15 fm, Oregon sta 276, 23 Feb 1951.—USLZ2920. 4 ♂; Wakulla Beach, D. H. Wilber and D. L. Felder, 3 Apr 1985.—USLZ2921. 2 ♂; same.—USLZ2922. 1 ♂; same.—USLZ2923. 2 ♂; same.—USLZ2924. 4 ♂; same.—USLZ2925. 6 ♂; same.—USLZ2926. 1 ♂, 1

♀; Florida State Univ. Marine Lab., D. L. Felder and J. M. Felder, 6 Apr 1985.—USLZ2913. 3 ♀; approximately 3 mi W and offshore of Florida State Univ. Marine Lab., Turkey Point, Franklin County, D. H. Wilber and D. L. Felder, 4 Apr 1985.—USLZ2914. 1 ♂, 1 ♀; same.—USLZ2915. 1 ♂, 6 ♀; same.—USLZ2916. 3 ♀; same.—USLZ2917. 2 ♂, 2 ♀ (1 ovig.); same.—USLZ2918. 1 ♂, 4 ♀ (1 ovig.); same.—USLZ2919. 1 ♂, 5 ♀ (3 ovig.); same.—USLZ2677. 2 ♂, 2 ♀ (1 ovig.); Bay Mouth Bar, vicinity of Alligator Point, J. W. Martin, Oct 1982.—USLZ2929. 2 ♂, juv; same.—USLZ2928. 2 ♂; Alligator Point, D. H. Wilber, 5 Apr 1985.—USLZ2927. 3 ♂, 2 ♀; same.—75789. 1 juv; Apalachicola, A. S. Pearse, 5 Jun 1935.—75790. 2 juv; same, 16 Jun 1935.—228510. 2 ♀ (ovig.); Florida, from Florida State Museum.

Results and Discussion

Our analysis suggests a highly significant morphological separation between two major populations that were formerly treated together as the species *M. mercenaria* (Table 3, Figs. 6–8). One of these populations—that ranging from North Carolina to peninsular Florida, the southeastern Gulf of Mexico and the western Caribbean Sea (Fig. 5)—has morphology and color pattern on the chelipeds like that of recently located syntypes designated by Say (1818) as *Cancer mercenaria*; it is to this group that we now restrict the name *M. mercenaria*. A second population, distinct from *M. mercenaria* in morphology and coloration, is distributed in Gulf of Mexico coastal waters from the northwestern Florida panhandle to Tamaulipas State, Mexico; it is this population that we assign to a new species, *M. adina*. Preliminary results from ongoing studies of this new species by ourselves and several collaborators indicate that it has unique characteristics in both physiology and larval development, but those topics will be reserved for future treatments.

Table 3.—Discriminant and correlation coefficients of variables listed in sequential pairings between Group 1 (*M. mercenaria*) and Group 2 (*M. adina*) by stepwise discriminant analysis. Analysis A corresponds to Fig. 8A, analysis B to Fig. 8B; statistics do not address ungrouped samples on upper axes of those figures. Values include unstandardized (Unstd. Disc. Coef.) and standardized (Std. Disc. Coef.) canonical discriminant function coefficients, along with pooled within-groups correlations between canonical discriminant functions and discriminating variables (Within-gps Correl. Coef.).

Variable selected	Unstd. Disc. Coef.*	Std. Disc. Coef.	Within-gps Correl. Coef.
Analysis A:			
R2	51.713	0.670	0.747
R4	-3.699	-0.355	-0.690
R1	26.094	0.502	0.575
R3	-7.577	-0.412	0.083
(Constant)	6.757		
Analysis B:			
R4	2.616	0.257	0.675
R2	-49.508	-0.799	-0.590
R5	0.588	0.753	-0.159
R3	8.488	1.227	-0.090
R1	-48.038	-1.226	-0.477
(Constant)	-3.789		

* Group centroids: Analysis A, Group 1 = -2.109; Group 2 = 1.501. Analysis B, Group 1 = 2.307, group 2 = -1.523.

Scatterplots and regression analyses of variables comprising each of the ratios of morphological characters (Figs. 6 and 7) indicated that all ratios gave significant separation of the hypothesized populations, though R4 was least significant in making this separation.

Recent studies of isozyme variations in populations of stone crabs (T. Bert, Yale University, pers. comm.) have suggested that a genetically divergent population of *M. mercenaria* occurs along the coast of Georgia and South Carolina, perhaps extending as far north as Charleston. Our prior examinations of specimens had revealed no consistent differences in morphology and coloration between individuals we had observed in the Charleston area and elsewhere in the restricted range of *M. mercenaria*. Nevertheless, we classified a large sample



Fig. 5. Gulf of Mexico, parts of western North Atlantic Ocean and Caribbean Sea showing diagrammed geographic ranges of: a, *Menippe mercenaria* (Say), restricted, from Cape Lookout, North Carolina around peninsular Florida, through the Bahamas and Greater Antilles including Saint Thomas, Virgin Islands, to Yucatan Peninsula, Mexico, and Belize; b, *M. adina* new species from northwestern Florida, around Gulf of Mexico to Tamaulipas State, Mexico; c, zone of hybridization in Apalachee Bay region of northwestern Florida.

of specimens from Charleston on the basis of weighted morphological characters used in our discriminant analysis (Fig. 8A). We deemed such an analysis to be particularly important, as the Charleston area appears to be a likely source for Say's syntypes of *M. mercenaria*.

Both the distribution of discriminant scores and the resultant centroid for the Charleston sample closely approximated values for Group 1, which was the remainder of the population that we herein assign to *M. mercenaria*. Furthermore, both the Charleston sample and Group 1 diverged from values for Group 2, which was made up of samples that we assign to *M. adina*. This classification analysis was able to as-

sign correctly over 98% of the Group 1 and Group 2 individuals to their a priori designations. From the resultant canonical correlation of 0.873, it is evident that about 76% of the separation between Groups 1 and 2 is explained by the four variables utilized in the analysis. Thus, on the basis of the morphological characters that we have analyzed, we find no support for taxonomic distinction of populations in the Charleston area from the remainder of materials assigned to *M. mercenaria*. However, our sample from further south, especially along the Georgia coast, was neither large nor extensive enough to exclude completely the possibility that divergent phenotypes occur in that region.

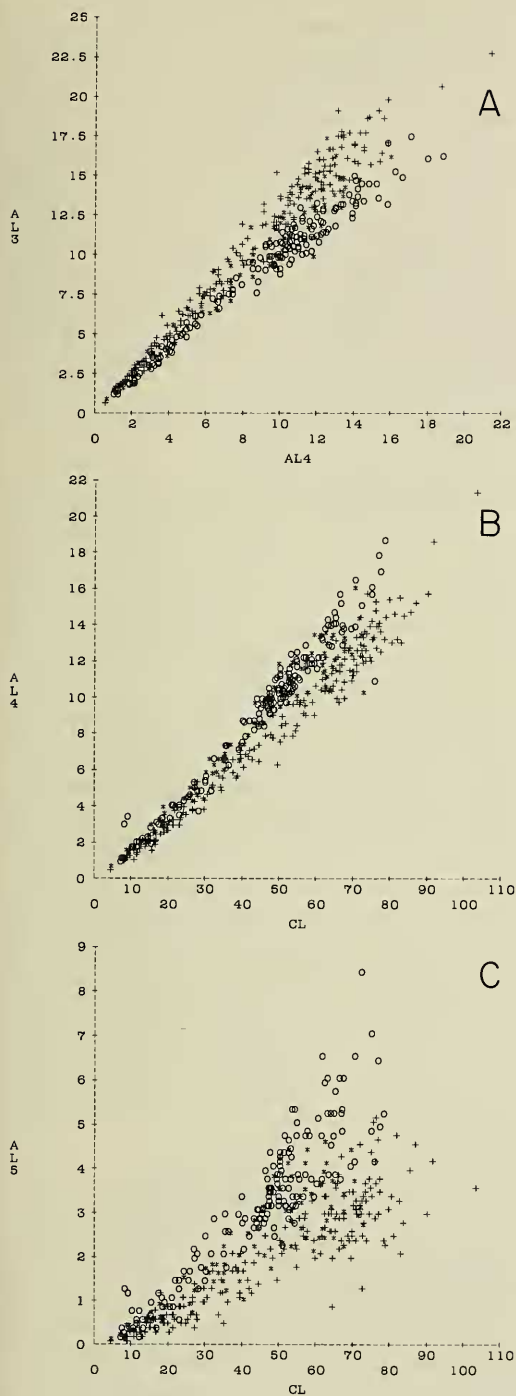


Fig. 6. Comparisons of morphological variables in *Menippe* populations assigned to *M. adina* (crosses), *M. mercenaria* (circles), and the hybrid zone (asterisks). A, Width anterolateral tooth 3 (AL3) as a function of

Atypical coloration of some specimens from the northeastern Gulf (Fig. 3c-f) first led us to suspect hybridization between populations in northwestern Florida. As early as 1979, we recognized the Apalachicola to Apalachee Bay region as the general area of transition or break between morphological extremes of "*M. mercenaria*," and noted that these two extremes appeared to differ somewhat in life history and habitat. However, not until adequate samples were measured and photographed did we conclude that introgressive hybridization between species was occurring there; simultaneously, an independent study of isozyme variations in populations of *Menippe* resulted in similar conclusions regarding populations in northwestern Florida (Bert, in press). Also supportive of this conclusion was evidence that stone crab fishermen in northwestern Florida have long recognized that a hybrid is involved in the fishery there. When asked to comment on coloration of local stone crabs in his catch (but otherwise unprompted), Mr. Clint Wood of Taylor Co., Fla., volunteered the following: "There is the 'dominicker' . . . spotted and with marks on the legs, there is the 'stone crab' . . . more solid brown . . . they catch more of them further to the west, and there is the 'cross' . . . a mix of the other two." He further noted that the "dominicker" was the only kind found south of Cedar Keys.

Small juvenile to large adult specimens were included in our two-group discrimi-

←
width anterolateral tooth 4 (AL4); *M. mercenaria*, $Y = 0.46776 + 1.18854 X$; *M. adina*, $Y = 0.66283 + 0.93972 X$; *M. hybrid*, $Y = 0.36809 + 1.05838 X$; B, Width AL4 as a function of carapace length (CL); *M. mercenaria*, $Y = -0.67632 + 0.18536 X$; *M. adina*, $Y = -0.73003 + 0.22309 X$; *M. hybrid*, $Y = -0.39580 + 0.20494 X$; C, Length AL5 (equal to $WLS - WBL5$ in Fig. 1) as a function of CL; *M. mercenaria*, $Y = -0.25118 + 0.04756 X$; *M. adina*, $Y = -0.45164 + 0.08246 X$; *M. hybrid*, $Y = -0.11821 + 0.05568 X$. All measurements in mm and taken as indicated in Fig. 1.

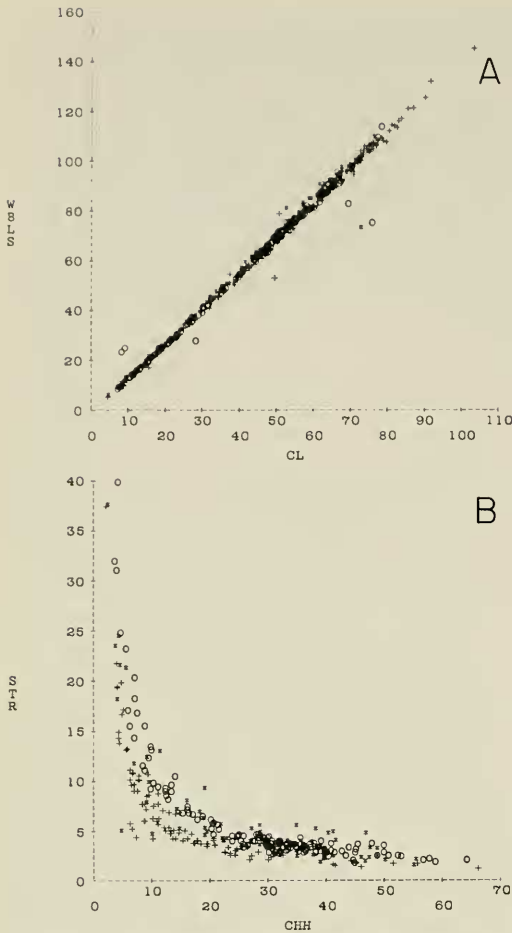


Fig. 7. Comparisons of morphological variables in *Menippe* populations assigned to *M. adina* (crosses), *M. mercenaria* (circles), and the hybrid zone complex (asterisks). All measurements in mm. A, Width of carapace excluding anterolateral tooth 5 (WBLS) as a function of carapace length (CL), taken as indicated in Fig. 1; *M. mercenaria*, $Y = -1.63382 + 1.42285 X$; *M. adina*, $Y = 0.04080 + 1.38674 X$; *M. hybrid*, $Y = -0.47386 + 1.40583 X$; B, Number of striae per mm (STR) in stridulatory patch on major chela as a function of maximum chela height (CHH), as shown in Fig. 2; *M. mercenaria*, $\ln Y = 4.07954 - 0.92235 \ln X$; *M. adina*, $\ln Y = 4.60272 - 0.94048 \ln X$; *M. hybrid*, $\ln Y = 4.07787 - 0.81343 \ln X$.

nant analysis of *M. mercenaria* and *M. adina*, and subsequent assignment of the sample from the hypothesized hybrid zone (Panama City to Steinhatchee, Fla.) (Fig. 8B). The analysis included five variables, all

of which provided for an increase in group separation. The analysis correctly classified 97% of individuals assigned a priori to Group 1 (*M. mercenaria*) or Group 2 (*M. adina*), thus demonstrating morphological distinction of these species over a broad range of size classes. The resultant canonical correlation of 0.883 indicates that about 78% of the separation between Groups 1 and 2 is thus explained. Exclusion of individuals less than 15 mm carapace length from the analysis improved correct classification to over 99% on the basis of the same five variables (data not figured).

Superposition of a sample from the hypothesized hybrid zone (Fig. 8B, upper axis) on discriminant scores from populations assignable to *M. mercenaria* and *M. adina* (lower axis) defines a broadly intermediate but morphologically heterogeneous group which appears to include *M. mercenaria*, *M. adina*, hybrids of the two, and possible backcrosses. However, when discriminant scores for this group are independently separated into subgroups based upon color, they resolve into means a, b, and c as indicated, where color morph "a" matches color of *M. adina*, "c" matches color of *M. mercenaria* and "b" is intermediate. The significance of differences among these three morphs is made clear by statistical comparisons among sample means of their discriminant scores: a, $\bar{x} = .79063 \pm \text{SD } .86266$ vs b, $\bar{x} = .51325 \pm \text{SD } 1.2334$, $t = -5.071$, 53 DF; b vs c, $\bar{x} = 1.76489 \pm \text{SD } .92149$, $t = -4.165$, 40 DF; $P < .01$.

The sample comprising subgroup "a" (Fig. 8B) of the hybrid zone population in our analysis is slightly larger than those comprising subgroups "b" and "c," and likely includes a few individuals from just west of the area in which introgression of the two species occurs. This consists of 11 specimens from the vicinity of Panama City, Fla. In retrospect, all the latter are assignable to *M. adina*, and we have to date obtained no hybrid specimens from west of Cape San Blas. Thus, while we include specimens from

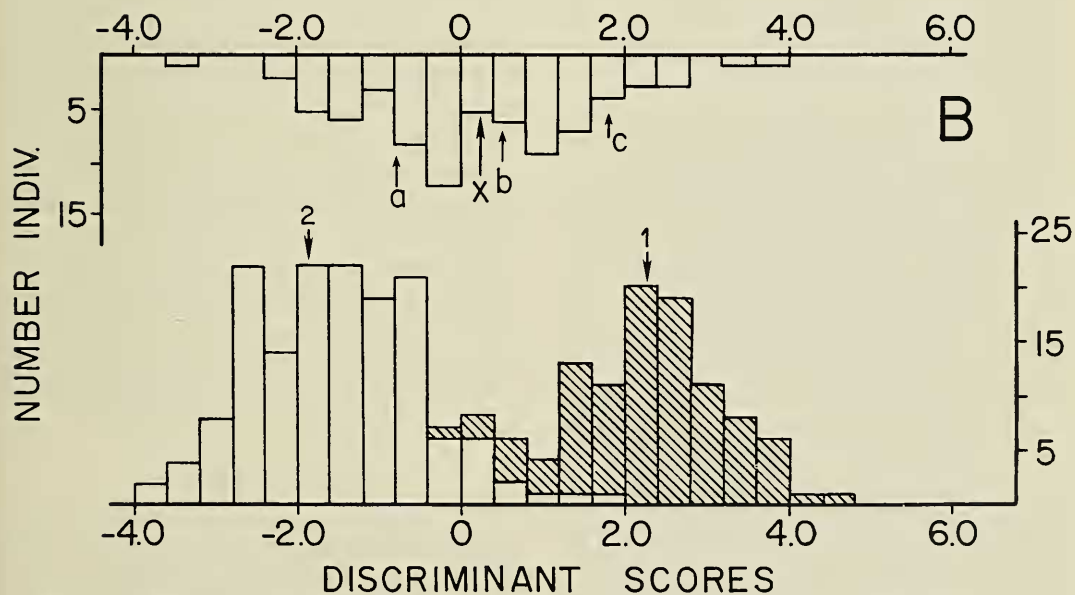
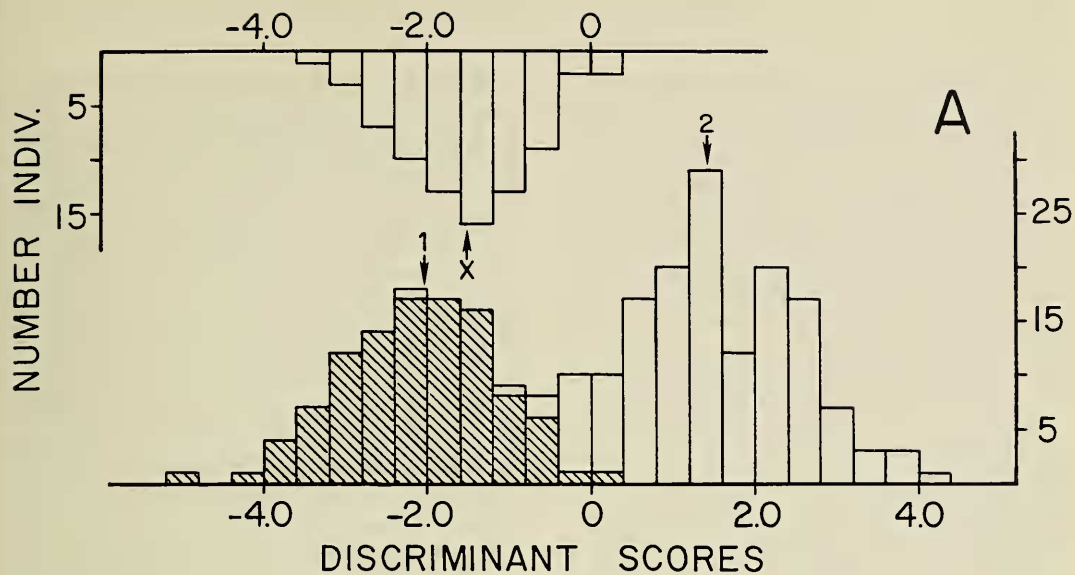


Fig. 8. A, Distribution of discriminant scores based upon R1, R2, R3 and R4 for specimens ≥ 15 mm carapace length: lower axis—*a priori* geographic Groups 1 and 2 (arrows mark centroids), assignable to *M. mercenaria* (cross-hatched bars) and *M. adina* (open bars), respectively; upper axis—ungrouped sample from Charleston, S.C. (arrow \times marks mean); B, Distribution of discriminant scores based upon R1, R2, R3, R4, and R5 for all sizes (excluding only specimens that lacked R5 data): lower axis—*a priori* Groups 1 and 2 (arrows mark centroids), assignable to *M. mercenaria* (cross-hatched bars) and *M. adina* (open bars), respectively; upper axis—ungrouped sample from northwest Florida (arrow \times marks overall mean; arrows a-c mark means for three color morphs).

Table 4. — Percentage of each color morph in samples of *Menippe* from two habitats in northwest Florida. Color morph "a" is that typical of *M. adina*, "c" is that typical of *M. mercenaria*, and "b" is intermediate and believed typical of hybrids; color patterns for morphs are described in Materials and Methods. Samples were taken on 3–4 April 1985; "oyster reef" habitat is located at Wakulla Beach, Wakulla Co.; "grass bed" habitat is located just west of the Florida State University Marine Laboratory, Turkey Point, Franklin Co.

Habitat	Color morph		
	a	b	c
Oyster reef n = 18	67	33	0
Grass bed n = 29	31	31	38

Panama City in the hybrid zone sample from northwest Florida, as defined for our present analysis, the actual western extreme can only be defined after much more thorough collecting in that area.

Although detailed studies of ecological and physiological differences between *M. mercenaria* and *M. adina* have not as yet been completed, evidence for such differences emerges from observation of habitats in which these species have been collected. In the northwestern Gulf of Mexico, *M. adina* inhabits oyster reefs, rock jetties, and other debris-cluttered substrates in shallow waters where salinities range from 35‰ to distinctly less than 10‰. Throughout its distribution, *M. mercenaria* seems instead to be restricted to the upper extreme of this salinity range, inhabiting rubble and debris much as does *M. adina*, but in most cases preferring grass beds to inshore oyster reefs. In the course of sampling two habitats within the northwest Florida hybrid zone, we observed the hybrid or intermediate color morph (morph "b") to be about as common in an inshore oyster reef habitat as it was in rubble on a much less euryhaline grass bed (Table 4); however, the *M. adina* color morph (morph "a") was more common on the euryhaline oyster reef than in the grass bed, and the *M. mercenaria* color morph

(morph "c") was common in our sample from the higher salinity grass bed but absent from the oyster reef. Although more extensive collections are needed to confirm the pattern suggested by these preliminary observations, it appears that genetic composition of a given sample from within the hybrid zone may, at least in part, be dictated by habitat. If so, systematic sampling from a full spectrum of habitats will be required in the course of further characterizing genetic trends within the zone of introgression, and characterizations of small or isolated samples cannot apply generally to the heterogeneous complex of the hybrid zone.

The recognition and separation of cryptic and sibling species among the Decapoda has been the subject of several recent investigations. For the most part, these are the subject of a forthcoming review (Knowlton, in press). In a number of cases, differences in coloration have provided the first evidence to support recognition of closely related siblings. This has been particularly true in recent studies of the pistol shrimp *Alpheus armatus* Rathbun and its near relatives (Knowlton and Keller 1985). In our studies, color not only facilitates the recognition of two closely related crab species; it also affords a character of use in recognition of what appear to be hybrids of these species. More detailed analysis of patterns may serve to distinguish simple hybrid crosses from possible backcrosses, and should afford a very useful phenological tool in future studies of genetic lineage.

Acknowledgments

We thank A. Bogen and G. Davis, Academy of Natural Sciences of Philadelphia for help in locating and authenticating the syntypes of Say's *C. mercenaria*. Mark Caldwell and E. M. Wenner, South Carolina Marine Resources Institute, provided specimens and measurements. David Camp, Florida Department of Natural Resources, arranged loans of specimens, and J. Forest provided photographs of selected specimens in the Muséum National d'Histoire

Naturelle, Paris. Charles Dugas, Louisiana Department of Wildlife and Fisheries, Jennifer M. Felder, Lafayette Natural History Museum, Ardis B. Johnston and H. W. Levi, Museum of Comparative Zoology, Harvard University, and Dara H. Wilber, Florida State University, assisted in collection and/or measurement of selected specimens. L. G. Abele and W. F. Herrnkind provided laboratory space and accommodations at the Florida State University Laboratory during field work there. Lee-Ann C. Hayek and Cindy A. Carman, Smithsonian Institution Office of Information Resource Management, and R. Sonnier, University of Southwestern Louisiana Computing Center, gave statistical counsel and ran the statistical analyses, with assistance from Ruth E. Gibbons who also drafted figures. S. Michaels, NMFS Southeast Fisheries Center provided fisheries statistics. Discussions with Dara H. Wilber, Harriet M. Perry, Gulf Coast Research Laboratory, T. M. Bert, Florida Department of Natural Resources, and critical reading by B. B. Collette, NMFS Systematics Laboratory, and R. B. Manning, USNM, benefitted the manuscript. Dactyls were drawn by Keiko Hiratsuka Moore. Virginia Thomas assisted with word processing. DLF was supported in part by funds from the NOAA Sanctuary Programs Division, under Cooperative Agreement No. NA83AA-H-CZ053, and by a grant from the Coypu Foundation.

For DLF this is contribution no. 9 from the USL Center for Crustacean Research.

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